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Research Document 2011/038

Document de recherche 2011/038

Gulf Region

Recent trends in abundance of larval anisakine parasites in southern Gulf of St. Lawrence cod (Gadus morhua), and possible effects of the parasites on cod condition and mortality

Tendances récentes concernant l'abondance des larves d'anisakinés parasites dans les morues du sud du golfe du Saint-Laurent (Gadus morhua) et incidence possible des parasites sur la condition et la mortalité de la morue

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ISSN 1499-3848 (Printed / Imprimé) ISSN 1919-5044 (Online / En ligne) Her Majesty the Queen in Right of Canada, 2011 © Sa Majesté la Reine du Chef du Canada, 2011





Correct citation for this publication:

McClelland, G., Swain, D.P., and Aubry, É. 2011. Recent trends in abundance of larval anisakine parasites in southern Gulf of St. Lawrence cod (*Gadus morhua*), and possible effects of the parasites on cod condition and mortality. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/038. iv + 30 p.

ABSTRACT

Larvae of the marine mammal parasites, Pseudoterranova decipiens, Anisakis simplex and Contracaecum osculatum, were surveyed in cod (Gadus morhua) from the southern Gulf of St. Lawrence between September, 2007 and May, 2009. In 2008-09, abundances of all three nematode species surged to levels unprecedented for Northwest Atlantic cod, an event that may be related to a warming trend in sea temperatures. A weak positive relationship between condition and intensity of infection was observed in both small and more heavily infected large southern Gulf cod. This relationship is likely indirect, resulting from variation in feeding intensity or foraging success among cod. Cod which consume more food are in better condition but acquire more parasites. There was no tendency for the relationship between condition and parasite abundance to become less positive over the winter period when little feeding occurs. These results do not preclude a direct negative effect of parasite infection on cod condition, but they do indicate that any such effect is weak relative to other factors affecting condition. Because sub-lethal effects should become apparent before lethal effects, these results also suggest that parasite-induced mortality related to direct damage to organs and tissues or depletion of energy reserves is small in this population. Analyses of changes in frequency distribution of parasite abundance with cod size or age do not appear to indicate mortality of heavily infected southern Gulf cod, but losses resulting from parasitism may be offset by increases in incidence of infection as cod grow and exploit more heavily infected prey. Analyses of worm count frequency distributions of larval anisakine nematodes have, however, provided evidence of parasite-induced mortality in cod from the Cape Breton and Central Scotian shelves, and in American plaice throughout the southern Gulf and Scotia-Fundy regions. Parasite infection may contribute to the elevated natural mortality of southern Gulf cod by increasing the susceptibility of heavily infected fish to predators.

RÉSUMÉ

Les larves des parasites des mammifères marins Pseudoterranova decipiens, Anisakis simplex et Contracaecum osculatum ont fait l'objet d'une étude portant sur la morue (Gadus morhua) du sud du golfe du Saint-Laurent entre septembre 2007 et mai 2009. En 2008-2009, l'abondance des trois espèces de nématodes s'est accrue subitement et a atteint des sommets jamais observés chez la morue de l'Atlantique Nord-Ouest. Il s'agit d'un événement qui pourrait être attribuable à une tendance au réchauffement des températures de l'océan. Il existe un faible lien positif entre l'intensité de l'infestation et la condition chez les petites ainsi que les grosses morues du sud du golfe chez lesquelles l'infestation était plus grave. Ce lien est vraisemblablement indirect et découlerait de variations dans l'intensité de l'alimentation ou le succès de la quête de nourriture chez la morue. Une morue qui consomme plus de nourriture affiche vraisemblablement une meilleure condition, mais est aussi contaminée par plus de parasites. Le lien entre l'abondance des parasites et la condition n'affichait aucune tendance et devenait moins positif durant l'hiver, lorsque les morues se nourrissent peu. Ces résultats n'écartent pas la possibilité d'effets négatifs directs de l'infestation par les parasites sur la condition de la morue, mais ils indiquent que de tels effets sont faibles comparativement à d'autres facteurs ayant une incidence sur la condition. Du fait que les effets sublétaux devraient devenir apparents avant les effets létaux, ces résultats laissent également sous-entendre que la mortalité induite par les parasites en raison des dommages directs causés aux organes et aux tissus ou en raison de l'épuisement des réserves d'énergie est faible dans cette population. Les analyses des changements dans la distribution des fréquences fondée sur l'abondance des parasites selon la taille ou l'âge de la morue ne semblent pas indiquer que les morues du sud du golfe gravement infestées en meurent, mais les pertes découlant du parasitisme pourraient être compensées par des augmentations de l'incidence de l'infestation au fur et à mesure que la morue croît et exploite des proies plus gravement infestées. Les analyses des distributions des fréquences fondées sur les dénombrements des vers de larves anisakinés nématodes ont cependant fourni des preuves de mortalité liée aux parasites chez les morues des plateaux du Cap-Breton et du centre du plateau néo-écossais ainsi que chez les plies canadiennes dans l'ensemble du sud du golfe et la région de Scotia-Fundy. L'infestation par les parasites pourrait contribuer à la mortalité naturelle élevée de la morue du sud du golfe en augmentant la vulnérabilité des poissons infestés face aux prédateurs.

1. INTRODUCTION

Infections with larval anisakine nematodes have proven a chronic and costly cosmetic problem for fish processors and may contribute to host mortality (McClelland 2002). Members of the fishing industry have also suggested that parasite infection may contribute to poor fish condition and growth.

In order to examine these possibilities, parasites were enumerated in southern Gulf of St. Lawrence cod (*Gadus morhua*) collected for monitoring of seasonal variation in condition between May 2007 and May 2009. Parasites were counted in 1,553 cod collected from May to November 2007 (see Fig. 1.1 for sample locations), 1,461 cod collected from May to September 2008 (see Fig. 1.2 for sample locations) and in 900 cod collected between April 30 and May 3, 2009. The 2009 sample was taken from 20 bottom-trawl tows made off north-western Cape Breton along the migration routes of cod returning to the southern Gulf in spring (i.e. in the Cape Breton Trough and along the southern slope of the Laurentian Channel between Cape Breton and the Magdalen Islands).

Three species of larval parasitic nematode were recorded: benthically transmitted "sealworm" (*Pseudoterranova decipiens*), and pelagically transmitted "whaleworm" (*Anisakis simplex*) and *Contracaecum osculatum*. Harp seal is the most important final host for the *C. osculatum*, although it also outnumbers *P. decipiens* in the stomachs of Gulf grey seals. As implied by its common name, the usual final hosts of *A. simplex* are cetaceans, while few of the large numbers of the whaleworm larvae which infect seals survive to maturity. In addition to parasite counts, fish length, fish weight and the weights of various body organs were measured and otoliths were removed for ageing (see Swain et al. (2011) for further details on the condition monitoring program).

2. ABUNDANCE OF LARVAL ANISAKINE PARASITES IN SOUTHERN GULF COD

In compliance with results of a stock delineation study using parasites as biological indicators (McClelland and Melendy 2011), September 2007 and 2008 samples of southern Gulf of St. Lawrence cod were partitioned into eastern and western components (Table 2.1). The majority of the cod, 79% and 93% in 2007 and 2008 respectively, were sampled from the south-western Gulf. As the 2009 sample was collected off north-west Cape Breton in late April and early May as cod returned to the southern Gulf after overwintering on the slopes of the Cape Breton Shelf and the neighboring portion of the eastern Scotian Shelf, it may have been comprised of both south-eastern and south-western Gulf cod as well as more heavily infected near-shore fish from both areas. Samples, including those collected during a 1980-81 survey conducted from commercial vessels and the 2004-05 stock delineation survey were compared by ANOVA following \log_{10} (n+1) transformation of nematode counts. Given a scarcity of larger cod in the 2004-05, 2007 and 2008 samples, analyses were confined to cod in the 30-50 cm length range, the same range used in the stock delineation study. The likelihood of host length effects within this range was not addressed at this time.

Contrasts of 1980-81 and 2007 data revealed that abundance (expressed as mean count) of larval P. decipiens was significantly greater ($P \le 0.0001$) in 2007 samples from both southwestern (Fig.2.1) and south-eastern Gulf cod (Fig. 2.2). A significant ($P \le 0.0001$) increase in abundance of larval A. simplex was also detected in the south-eastern Gulf cod in 2007 (P = 0.0001), but not in south-western Gulf cod (P = 0.51). There was also no difference between the two surveys in regard to abundance of C. osculatum in south-eastern and south-western Gulf

cod. Contrasts with data from the stock delineation study further revealed that, except for a decline in P. decipiens abundance in south-eastern Gulf cod in 2007 (P = 0.0019), P. decipiens and A. simplex abundances recorded in 2007 were consistent with those found in 2004-05. On the other hand, there were significant declines in C. osculatum abundances in 2007 samples of both south-western (P \leq 0.0001) and south-eastern Gulf cod (P = 0.0002), and as a consequence, the 2007 C. osculatum data were deemed unreliable and excluded from further analyses.

In 2008-09, abundances of all three nematode species surged to levels unprecedented in Northwest Atlantic cod (Figs. 2.1 to 2.3; Tables 2.1 and 2.2), with increases in abundance, recorded in 2008 south-western and south-eastern Gulf cod samples being highly significant (P ≤ 0.0001). Further, current abundances of P. decipiens and A. simplex in southern Gulf cod greatly exceed those found in cod sampled from the Cape Breton Shelf, Sable Island Bank and south-western Nova Scotia in 2006 (Fig. 2.4), and in a 1990 cod sample from Sable Island Bank which had been the most heavily infected sample reported to this point. Abundances of C. osculatum which is rarely found in fish south of the Cape Breton Shelf (McClelland 2008) were not compared here. Nematode abundances in cod sampled in spring 2009 seemed intermediate to those found in south-western and south-eastern Gulf cod sampled in September 2008 suggesting mixing between eastern and western stock components. Differences in sealworm abundance between the 2009 sample and western and eastern components of the 2008 sample were not significant, but disparities of modest significance were apparent in contrasts of A. simplex and C. osculatum abundances; A. simplex was more numerous in cod sampled from the eastern Gulf in 2008 than in the 2009 sample (P = 0.0102). While C. osculatum enumerated from the 2009 sample outnumbered those found in south-eastern Gulf cod sampled in 2008 (P = 0.0164), they were less numerous than those found in south-western Gulf cod in 2008 (P = 0.0276). These findings support the contention that the 2009 sample was comprised of both western and eastern Gulf cod. Records from earlier surveys indicated that C. osculatum is found more frequently in south-western than in south-eastern Gulf cod. The whaleworm A. simplex has recently become more abundant in the south-eastern Gulf cod, possibly as a consequence of the growth of the local pilot whale population.

Larval sealworm were most numerous in the fillets of small southern Gulf cod, but became increasingly prevalent in the belly flaps and body cavities of larger, heavily infected fish. Of the 713 P. decipiens enumerated in cod \geq 71 cm in length (n = 8) in the 2009 sample, 53% occurred in the napes, 36% in the filets, and 11% in the body cavity. Although often numerous in the napes of heavily infected fish, A. simplex primarily occurred in the viscera. C. osculatum were similarly confined to the body cavity, usually being found among the pyloric caecae. Density of P. decipiens infection in cod \geq 51 cm in length from the 2009 southern Gulf sample was 15.41 worms per kg (n = 137) compared to 8.41 worms per kg for 51+ cm cod (n = 100) from Sable Island Bank in 1990, the heaviest infections previously recorded in eastern Canadian cod.

Infections with larval anisakine nematodes have proven a chronic and costly cosmetic problem for fish processors (McClelland 2002). Density of larval sealworm in filets of 51+ cm fish from the 2009 sample was 32.45 worms per kg of filet, greatly exceeding the old 'Fish Inspection' tolerance of 5 worms per 15 lb block of filets (0.73 per kg) by a factor of 44 (McClelland et al. 1983).

While there is little or no information on larval sealworm abundance in southern Gulf cod between the early 1980s and 2004-05, a time series monitoring spatial and temporal distributions of sealworm in an indicator host, American plaice, revealed a sharp decline in

sealworm abundance between the late 1990s and mid 2000s (Fig. 2.5). These declines occurred not only in southern Gulf plaice, but also in plaice from the Cape Breton and central and eastern Scotian shelves, and were probably related to a cold event lasting approximately a decade, from the late 1980s to the late 1990s. During the cold event, near bottom temperatures $\leq 0^{\circ}$ C persisted over much of the southern Gulf throughout the year. Since prolonged exposure to a temperature of 0° C is lethal to sealworm eggs, transmission of the parasite would have been confined to shallow in-shore waters in summer. Increases in sealworm abundance evident in 2006 plaice samples from the Cape Breton, however, probably reflect the more recent warming trend. Hence the recent surge in abundances of larval anisakine nematodes in southern Gulf cod may have as much to do with climatic events as with growth of marine mammal (seal and pilot whale) populations.

In 2008-09, abundances of all three nematode species in southern Gulf cod surged to levels unprecedented for Northwest Atlantic cod, an event that may be more attributable to a warming trend in sea temperatures than to the growth of marine mammal populations.

3. EFFECTS OF INFECTION BY ANISAKINE PARASITES ON CONDITION OF SOUTHERN GULF COD

An effect of parasite infection on fish condition could result from the same mechanisms that may increase host mortality (McClelland 2002, and references therein). Feeding parasite larvae consume a portion of the energy acquired by their host, while migrating and feeding larvae may also damage vital host organs, impairing the host's ability to forage (and escape predators). Host foraging success and predator avoidance may also be chemically impaired by their sealworm parasites. Larval sealworms secrete volatile ketones which may act as local anaesthetics. Declines in maximum swimming speed with increasing intensity of parasite infection have been observed in European smelt (Sprengel and Lüchtenberg 1991). Reduced foraging ability of hosts due to parasite infection would be expected to result in a negative relationship between host condition and intensity of parasite infection.

3.1 ANALYSIS OF THE 2007 AND 2008 DATA

Data were analyzed using the following model:

$$\log_e Y_{ii} = \beta_0 + \beta_{1i} + \beta_2 \log_e L_{ii} + \beta_3 X_{ii} + \varepsilon_{ii}$$
 (3.1)

where Yij is either carcass weight (total weight – liver weight – gonad weight – stomach weight) or liver weight of fish j caught in month i, Lij is the length of this fish, and Xij is its parasite count. The effect of parasite count was assumed to be linear, but additional analyses were conducted with parasite count grouped into 2 or 4 levels and treated as a factor (like month) rather than a linear covariate. These additional analyses lead to conclusions similar to those of the analysis above. The September data were divided into separate eastern and western samples, which were treated as different levels of the "month" factor. Separate analyses were conducted for small (30-44 cm in length) and large (\geq 45 cm in length) cod because of the possibility that parasite effects would be important only in large cod whose parasite infections reached much higher levels of abundance than did those of small cod.

Results were similar between size classes of cod and between years. Effects of month and the covariate log_eL were highly significant in all analyses. The relationship between parasite abundance and host condition was positive in 26 of 28 cases, and significant at the 0.05 level in 13 of these cases (Table 3.1).

A significant positive relationship between sealworm (*P. decipiens*) abundance and carcass weight occurred for both small and large cod in both 2007 and 2008. Although highly significant (when modelled as a linear covariate), the variation in condition accounted for by this factor was generally much smaller than the seasonal change in condition (Figs. 3.1 and 3.2). Small cod in 2008 were an exception. In this case, the difference in condition between cod with the lowest and highest levels of infection was comparable to the difference in condition between May and September. In contrast to the relationship with sealworm abundance, carcass weight was unrelated to the abundance of *Anisakis*, and showed a marginally significant negative relationship with the abundance of *Contracaecum* in small cod (Table 3.1).

Like carcass weight, liver weight was positively related to sealworm abundance, but the relationships were weaker and statistically significant for only large cod (Table 3.1). On the other hand, relationships between condition and *Anisakis* abundance were stronger for liver weight than for carcass weight, though this relationship was statistically significant only for small cod in 2007. The positive relationship between liver weight and total parasite abundance was statistically significant for both small and large cod in both 2007 and 2008. Again, parasite effects were relatively small compared to seasonal changes in condition (Fig. 3.3 and 3.4).

These results indicate a weak positive relationship between the intensity of parasite infection and the condition of southern Gulf cod. This is in the direction opposite to that expected for direct effects of parasite infection on condition. A likely explanation is that this positive relationship is an indirect effect of variation in feeding intensity and foraging success among cod. Individuals that forage more intensely or successfully acquire more energy and thus are in better condition. However, in the process of eating more food, they also consume more parasites. These results do not preclude direct negative impacts on condition. More successful foragers might be in even better condition if they were not heavily infected by these parasites. However, the results do suggest that any direct negative effects of parasite infection are small compared to the effects of individual variation in foraging success due to other factors.

3.2 COMPARISON OF PARASITE EFFECTS BETWEEN SPRING AND FALL SAMPLES

Southern Gulf cod exhibit a strong seasonal cycle in condition (Schwalme and Chouinard 1999). These cod feed little over the winter, resulting in declining condition during the winter period. Negative effects of parasite infection on condition might be more evident following the overwinter fasting period. For example, cod in better condition in the fall tend to be more heavily infected by parasites; condition may decline more rapidly over winter in these heavily infected fish than in the lower-condition fish which also tend to have fewer parasites. If so, the strength of the positive relationship between condition and intensity of parasite infection would be expected to decline over winter.

To examine this possibility we compared the relationship between condition and parasite load between September samples and the large sample collected in early May 2009. Two sets of analyses were conducted. The first compared the September 2008 data to the May 2009 data (Table 3.2). The second combined September data from both 2007 and 2008 but excluded *Contracaecum* from the analysis since this parasite was not reliably enumerated in 2007 (Table 3.3). The model used was like that described by equation 3.1, except that separate slopes for the parasite covariate were estimated for May and September. Three size classes of cod were examined: small, large and all sizes combined.

There was no overall tendency for the slope of the parasite effect to be less positive in May than in September (Tables 3.2 and 3.3). In the first analysis, there were 24 comparisons (Table 3.2). The slope was more positive in September in 8 cases and more positive in May in 16 cases. However, most of these differences were not statistically significant. Slopes differed significantly at the 0.05 level in 9 of the 24 cases (without correction of the critical level for multiple tests). Of these 9 cases, slopes were greater in September in 2 cases and greater in May in 7 cases.

Results were similar with the addition of the 2007 September data (Table 3.2). Slopes were more positive in September in 8 cases and in May in 10 cases. Only four of these differences were statistically significant at the 0.05 level (again without correction for multiple tests), two with greater slopes in September and two with greater slopes in May.

3.3 CONCLUSION

We were unable to detect a negative effect of parasitic infection on cod condition, despite large sample sizes. This indicates that any effect must be small and less important than other sources of variation in condition, such as variation in foraging rate or success. It also suggests that parasite-induced mortality related to direct injury of organs and tissues, depletion of energy reserves or chemical impairment of foraging success is small in this population, since sub-lethal effects (e.g., on condition) should become apparent before lethal effects. It does not, however, preclude the possibility of mortality due to the negative effect of the parasites' ketone secretion on predator avoidance. Ketone secretion seems typical of host behavioural-altering mechanisms which parasites have evolved to promote their transmission to subsequent (intermediate or final) hosts. Given the possibility that seals may frequently consume only the bellies of larger cod, concentration of larval *P. decipiens* in the napes (belly flaps) of large cod (53% of the sealworm in southern Gulf cod >70 cm in length; Fig. 3.5) may similarly serve to maximize parasite transmission.

4. PARASITE-INDUCED MORTALITY OF SOUTHERN GULF COD

To look for evidence of parasite-induced mortality of southern Gulf cod, we examined how the frequency distribution of parasite abundance changed over time within cohorts of cod. This distribution is typically strongly skewed, with a long upper tail. If parasite infection increases the risk of mortality, this risk would be expected to be greatest in the most heavily infected individuals. Thus, parasite-induced mortality should be evident as a loss of individuals over time from the upper tail of the distribution of parasite abundance.

Parasite-induced mortality might be most evident over winter when cod feed little. To examine this, we compared parasite abundance distributions between cod collected during the synoptic bottom-trawl survey in September 2008 and those collected the following spring. Parasites were enumerated in length-stratified samples from each catch of cod in the September survey. Thus this collection should provide a reasonable description of levels of parasite infection in the southern Gulf population in September 2008. The spring 2009 collection consisted of length-stratified samples of cod catches in a small survey (20 bottom-trawl tows) conducted in the migration pathways used by cod as they return to the southern Gulf in spring (i.e., in the Cape Breton Trough and along the south slope of the Laurentian Channel). The intent was to obtain a comprehensive sample from the population (to the extent possible, given logistic constraints). However, a portion of the population would have passed through the surveyed area prior to the April 30 – May 03 sampling period. The extent to which this biased the sample is not known. Although cod condition declines substantially between September and the following spring in

this population (see Swain et al. 2011), some feeding would have occurred between the September and spring samples.

Figures 4.1 to 4.4 compare the frequency distributions of abundance of *Pseudoterranova* and *Anisakis* counts between September 2008 and May 2009 along cohort groups. In all cases, instead of decreasing due to mortality of heavily infected cod, the proportion of cod with high parasite abundance (i.e., the proportion of cod occurring in the upper tail of parasite abundance) appeared to increase between September 2008 and the following May. Given that Gulf cod feed little over winter, it seems unlikely that feeding in October and November 2008 would be sufficient to produce these increases in abundance of the two species. Disparities in nematode abundance in the two samples may be attributable to the fact that September 2008 sample was primarily comprised of cod from the south-western Gulf (n=1,351), while the Spring sample may have included more heavily infected eastern Gulf and near-shore fish. Nonetheless, there was no indication of loss of very heavily infected cod over winter.

Figures 4.5 and 4.6 compare abundances of *Pseudoterranova* and *Anisakis*, respectively, in older cod in the same cohorts between 2007 and 2008. The seasonal and spatial distributions of samples were similar between the two years (Figs. 1.1 and 1.2), except that there was no November sample in 2008 and there was a smaller proportion of eastern fish in the September 2008 sample than in the September 2007 sample. Again, there is no indication of a loss of very heavily infected fish over time from 2007 to 2008. Instead, the proportion of very heavily infected cod increased from 2007 to 2008, in conjunction with an increase in average parasite abundance. Results are similar for the analysis restricted to older fish (i.e. comparing ages 8+ in 2007 to 9+ in 2008).

Parasite abundance (mean count) increases with cod length (e.g., Fig. 4.7). If very heavily infected cod die, the ratio of variance to abundance would be expected to decline at large cod sizes due to the loss of the very heavily infected cod in the tail of the distribution of parasite intensity. In contrast to this expectation, the variance/abundance ratio increases to high values in the largest cod in all three years sampled (2007-2009; Fig. 4.7). In larger cod, however, loss of heavily infected fish from the tails of frequency distributions may be offset by the increasing incidence of infection (rate of re-infection) related to a (piscivorous) diet of more heavily infected prey. Further, as apparent from the increases in parasite abundance from 2007 to 2008, incidence of the three parasite species is accelerating in both larger and smaller cod. The confluence of sealworm variance/abundance ratios on host length trends at a host length of 50 cm (Fig. 4.7) might be indicative of mortality in smaller fish. Lastly, in other studies (McClelland 2002, 2008), analyses of nematode frequency distributions indicate that anisakine- induced mortalities have occurred in cod from the Cape Breton Shelf and Sable Island Bank, and in American plaice throughout the southern Gulf and Scotia-Fundy areas.

Analyses of variations in the frequency distribution of parasite intensity with cod size or age seem to provide little evidence of mortality of heavily infected cod. Yet, given the limitations of the data and evidence of sealworm-induced mortality in other cod stocks and American plaice, the possibility of mortality through the impact of parasite mediated ketones on predator avoidance cannot be dismissed.

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Table 2.1. Abundances of larval anisakines in 2007, 2008 and 2009 samples of 4T cod.

Year	1	Area	Cod	n	Nematode abundance ± s.e. (Maximum intensity)				
season			length (cm)		P. decipiens	A. simplex	C. osculatum		
2007	1	4T	≤15	26	0	0.04 ± 0.04 (1)	0		
Summer		West	16-20	14	0.14 ± 0.10 (1)	0	0		
			21-25	18	0.22 ± 0.12 (2)	0.06 ± 0.06 (1)	0		
			26-30	80	0.73 ± 0.11 (4)	0.48 ± 0.10 (4)	0.01 ± 0.01 (1)		
			31-35	208	0.87 ± 0.08 (6)	0.74 ± 0.11 (13)	0.07 ± 0.03 (4)		
			36-40	196	2.21 ± 0.19 (20)	1.26 ± 0.20 (25)	0.13 ± 0.03 (6)		
			41-45	235	3.47 ± 0.22 (27)	1.47 ± 0.16 (19)	0.31 ± 0.09 (13)		
			46-50	259	4.88 ± 0.30 (32)	1.72 ± 0.17 (24)	0.50 ± 0.10 (16)		
			51-55	143	6.31 ± 0.51 (36)	1.80 ± 0.21 (16)	$0.85 \pm 0.14 (8)$		
			56-60	42	$9.00 \pm 1.09 (38)$	1.98 ± 0.28 (6)	1.02 ± 0.26 (7)		
			≥61	16	19.13 ± 6.18 (98)	7.63 ± 2.23 (25)	2.06 ± 0.81 (9)		
		4T	≤20	66	0.30 ± 0.07 (2)	$0.11 \pm 0.04(1)$	0.02 ± 0.02 (1)		
		East	21-25	22	$0.36 \pm 0.14(2)$	0.05 ± 0.05 (1)	0.		
			26-30	26	1.08 ± 0.31 (7)	1.08 ± 0.32 (5)	0.12 ± 0.08		
			31-35	71	1.46 ± 0.17 (7)	1.54 ± 0.21 (7)	0.06 ± 0.03 (1)		
			36-40	28	2.79 ± 0.70 (16)	3.25 ± 0.91 (24)	0		
			41-45	40	2.60 ± 0.52 (13)	1.88 ± 0.44 (12)	0.28 ± 0.13 (4)		
			46-50	36	3.53 ± 0.49 (13)	1.69 ± 0.33 (9)	0.61 ± 0.20 (5)		
			51-55	19	$3.95 \pm 0.90 (17)$	2.16 ± 0.47 (6)	0.47 ± 0.21 (3)		
			≥56	8	$7.25 \pm 1.68 (16)$	$4.00 \pm 1.49 (14)$	0.38 ± 0.26 (2)		
2008	1	4T	≤15	27	0.26 ± 0.01(2)	0	0.04 ± 0.04 (1)		
Summer		West	16-20	30	0.33 ± 0.12 (2)	0.07 ± 0.07 (2)	0		
			21-25	41	1.24 ± 0.25 (9)	0.68 ± 0.33 (13)	0.05 ± 0.05 (2)		
			26-30	104	1.10 ± 0.13 (5)	2.03 ± 0.40 (27)	0.89 ± 0.15 (8)		
			31-35	115	2.33 ± 0.27 (17)	4.59 ± 0.47 (23)	1.46 ± 0.20 (13)		
			36-40	197	2.62 ± 0.19 (16)	6.38 ± 0.58 (66)	2.43 ± 0.26 (28)		
			41-45	273	5.88 ± 0.26 (26)	6.10 ± 0.35 (33)	3.05 ± 0.22 (18)		
			56-50	338	9.22 ± 0.31 (34)	7.57 ± 0.39 (65)	5.20 ± 0.39 (84)		
			51-55	162	11.23 ± 0.99 (145)	10.93 ± 0.73 (57)	11.30 ± 0.86 (55)		
			56-60	52	13.50 ± 1.47 (54)	17.69 ± 1.90 (76)	19.23 ± 3.05 (115		
			≥61	14	32.07 ± 7.69 (96)	31.71 ± 8.73 (120)	19.00 ± 4.18 (60)		
		4T	≤20	6	1.67 ± 0.33 (3)	0	0		
		East	21-25	32	1.25 ± 0.30 (7)	3.38 ± 0.99 (24)	0.09 ± 0.05 (1)		
			26-30	11	0.83 ± 0.21 (2)	2.82 ± 1.21 (12)	0.27 ± 0.25 (3)		
			31-35	12	3.92 ± 0.69 (7)	7.42 ± 1.56 (19)	0.25 ± 0.18 (2)		
			36-40	20	3.40 ± 0.53 (7)	$7.80 \pm 1.56 (28)$	1.35 ± 0.41 (7)		
			41-45	9	4.22 ± 0.66 (8)	22.11 ± 7.96 (81)	2.78 ± 1.13 (8)		
			46-50	13	9.46 ± 1.72 (21)	10.62 ± 4.17 (58)	$3.36 \pm 1.32 (17)$		
			≥51	5	46.00 ± 20.45 (106)	29.65 ± 16.54 (77)	5.50 ± 1.66 (10)		

Table 2.1 (continued).

Year / season	Area	Cod length (cm)	n	Nematode abundance ± s.e. (Maximum intensity)				
				P. decipiens	A. simplex	C. osculatum		
2009/	4T	21-25	23	1.30 ± 0.41 (7)	2.83 ± 1.19 (25)	0.30 ± 0.13 (2)		
Spring	East	26-30	110	1.13 ± 0.12 (5)	3.47 ± 0.53 (34)	0.68 ± 0.16 (13)		
		31-35	145	2.21 ± 0.23 (16)	2.47 ± 0.23 (13)	1.30 ± 0.20 (16)		
		36-40	162	4.38 ± 0.49 (56)	7.88 ± 0.80 (82)	2.18 ± 0.25 (19)		
		41-45	169	$7.97 \pm 0.46 (31)$	7.89 ± 0.80 (40)	3.62 ± 0.31 (27)		
		46-50	155	12.39 ± 0.65 (45)	10.05 ± 0.75 (50)	$5.12 \pm 0.59 (57)$		
		51-55	70	18.39 ± 1.51 (83)	13.50 ± 1.60 (87)	4.10 ± 0.49 (18)		
		56-60	36	24.44 ± 2.90 (64)	24.25 ± 2.98 (85)	20.58 ± 6.43 (207)		
		61-65	12	32.83 ± 3.38 (52)	39.25 ± 7.83 (83)	9.75 ± 1.85 (19)		
		66-70	11	43.73 ± 3.70 (69)	82.91 ± 30.04 (368)	15.55 ± 6.84 (76)		
		≥71	8	89.13 ± 19.41 (167)	118.13 ± 28.94 (76)	23.75 ± 12.65 (76)		

Table 3.1. Effect of parasite abundance on indices of condition of southern Gulf cod. Values are the slope parameter β_3 in equation 3.1 in the text, with its significance level in parentheses. Results are from an analysis of covariance with month (May – November) as a factor and log length and parasite abundance as covariates. Effects of month and log L were highly significant in all cases. The combined parasite analysis includes C. osculatum in 2008 but not 2007. Bold type indicates a significant difference at the 0.05 probability level

Variable	Cod size	Year	P. de	cipiens	A. si	mplex	C. os	culatum	All p	arasites
Carcass weight	Small	2007	0.0011	(0.044)	0.0002	(0.75)			0.0006	(0.097)
		2008	0.0018 (<0.0001)	0.0001	(0.51)	-0.0009	(0.047)	0.0003	(0.12)
	Large	2007	0.0007	(0.0050)	-0.0003	(0.56)		(/	0.0005	(0.030)
		2008	0.0005	(0.0013)	0.00005	(0.70)	0.00002	(88.0)	0.0001	(0.064)
Liver weight	Small	2007	0.0026	(0.29)	0.0058	(0.013)			0.0044	(0.0096)
		2008	0.0026	(0.16)	0.0015		0.0017	(0.38)	0.0018	(0.018)
	Large	2007	0.0029	(0.014)	0.0026	(0.32)		,/	0.0025	(0.013)
		2008	0.0018	(0.014)	0.0010	(0.12)	0.0012	(0.056)	0.0012	(0.0014)

Table 3.2. Slope of the relationship between indices of condition and intensity of parasite infection for cod collected in September 2008 or May 2009. The indices of condition are carcass weight and liver weight (with effects of fish size and season controlled statistically – see equation 3.1 in the text). P values indicate the significance of the overall slope and the difference in slope between September and May. Bold type indicates a significant difference at the 0.05 level.

Variable	Cod size	Statistic	P. decipiens	A. simplex	C. osculatum	Total
Weight	All	Sep slope	0.00133	-0.00014	-0.00060	0.00014
		May slope	0.00063	0.00041	0.00004	0.00026
		P slope	< 0.0001	0.0032	0.48	0.0010
		P interaction	0.088	0.073	0.15	0.50
	Small	Sep slope	0.00599	0.00069	-0.00229	0.00121
		May slope	0.00043	-0.00018	0.00042	0.00007
		P slope	0.0016	0.56	0.36	0.089
		P interaction	< 0.0001	0.21	0.093	0.043
	Large	Sep slope	0.00109	-0.00079	-0.00038	-0.00003
		May slope	0.00086	0.000488	-0.00002	0.00038
		P slope	0.0001	0.011	0.59	0.0013
		P interaction	0.65	0.0009	0.44	0.065
Liver	All	Sep slope	0.00127	0.00099	-0.00569	-0.00020
		May slope	0.00216	0.00353	0.00176	0.00188
		P slope	0.046	< 0.0001	0.73	< 0.0001
		P interaction	0.68	0.13	0.0017	0.032
	Small	Sep slope	0.01062	0.00549	-0.00482	0.00555
		May slope	0.00052	0.00342	0.01185	0.00390
		P slope	0.32	0.019	0.29	0.0040
		P interaction	0.13	0.57	0.048	0.57
	Large	Sep slope	0.00360	-0.00196	-0.00480	-0.00035
		May slope	0.00485	0.00463	0.00165	0.00330
		P slope	0.0008	< 0.0001	0.90	< 0.0001
		P interaction	0.66	0.0024	0.016	0.0030

Table 3.3. Slope of the relationship between indices of condition and intensity of parasite infection for cod collected in September 2007 and 2008 or May 2009. The indices of condition are carcass weight and liver weight (with effects of fish size and season controlled statistically – see equation 3.1 in the text). P values indicate the significance of the overall slope and the difference in slope between September and May. Bold type indicates a significant difference at the 0.05 level.

Variable	Cod size	Statistic	P. decipiens	A. simplex	Total	
Weight	All	Sep slope	0.00188	0.00006	0.00063	
		May slope	0.00144	0.00071	0.00070	
		P slope	< 0.0001	0.0002	< 0.0001	
		P interaction	0.40	0.10	0.81	
	Small	Sep slope	0.00521	0.00075	0.00159	
		May slope	0.00072	-0.00008	0.00017	
		P slope	0.0076	0.52	0.051	
		P interaction	0.0080	0.42	0.094	
	Large	Sep slope	0.00159	-0.00019	0.00048	
		May slope	0.00111	0.00064	0.00065	
		P slope	< 0.0001	0.0006	< 0.0001	
		P interaction	0.32	0.033	0.53	
Liver	All	Sep slope	0.00394	0.00190	0.00248	
		May slope	0.00662	0.00527	0.00434	
		P slope	< 0.0001	< 0.0001	< 0.0001	
		P interaction	0.18	0.27	0.076	
	Small	Sep slope	0.01133	0.00602	0.00687	
		May slope	-0.00006	0.00306	0.00224	
		P slope	0.054	0.0062	0.0015	
	P interaction		0.036	0.36	0.085	
	Large	Sep slope	0.00599	0.00097	0.00274	
		May slope	0.00709	0.00565	0.00511	
		P slope	< 0.0001	< 0.0001	< 0.0001	
		P interaction	0.65	0.013	0.060	

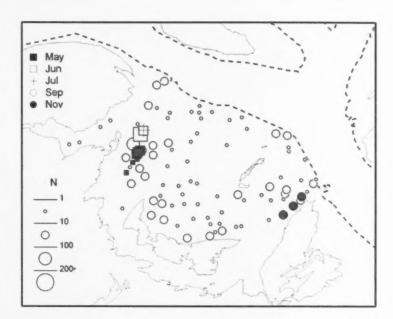


Figure 1.1 Locations of cod samples examined for parasites in 2007. Symbol size is proportional to sample size.

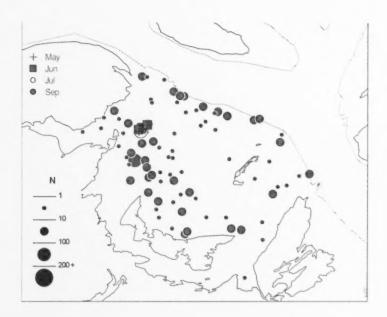


Figure 1.2. Locations of cod samples examined for parasites in 2008. Symbol size is proportional to sample size.

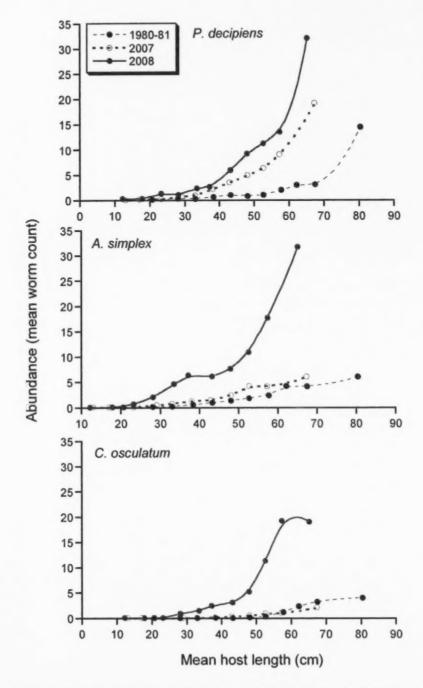


Figure 2.1. Abundances of Pseudoterranova decipiens, Anisakis simplex and Contracaecum osculatum larvae in five-cm length groups of cod sampled from the south-western Gulf of St. Lawrence in 1980-81 (n = 652), 2007 (n = 1,237), and 2008 (n = 1,351).

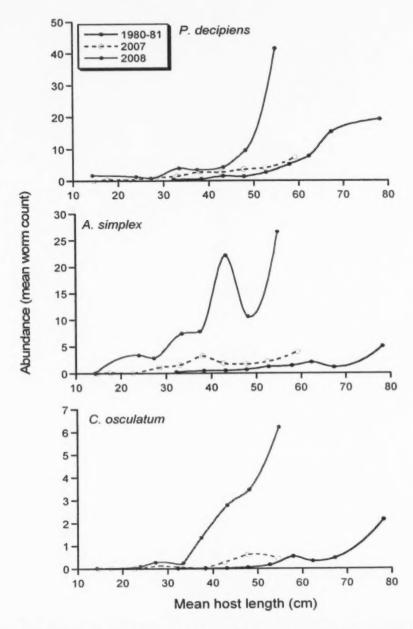


Figure 2.2. Abundances of Pseudoterranova decipiens, Anisakis simplex and Contracaecum osculatum larvae in five-cm length groups of cod sampled from the south-eastern Gulf of St. Lawrence in 1980-81 (n = 686), 2007 (n = 322), and 2008 (n = 108).

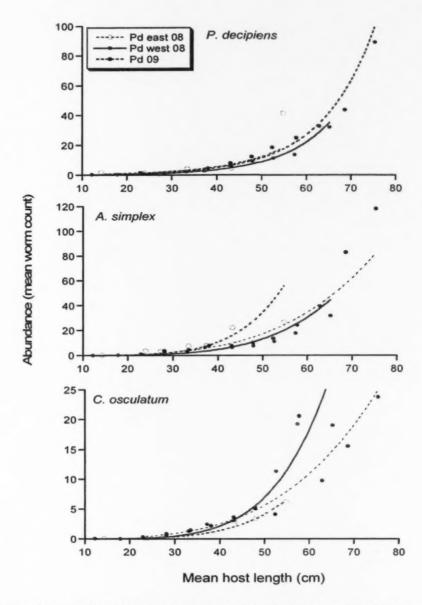


Figure 2.3. Abundances of Pseudoterranova decipiens, Anisakis simplex and Contracaecum osculatum larvae in five-cm length groups of cod sampled from the south-western Gulf of St. Lawrence in September, 2008 (Pd west 08; n = 1,351), the south-eastern Gulf in September 2008 (Pd east 08; n = 108) and from the south-eastern Gulf in April-May, 2009 (Pd 09; n = 902).

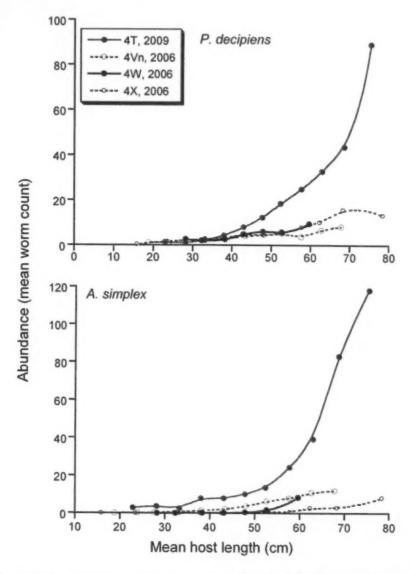


Figure 2.4. Abundances of larval P. decipiens and A. simplex in 5 cm length groups of cod collected from the southern Gulf of St. Lawrence (NAFO subdivision 4T) in 2009 (n = 902), and the Cape Breton Shelf (4Vn) (n = 526), Sable Island Bank (4W) (n = 279) and south-western Nova Scotia (4X) (n = 597) in 2006.

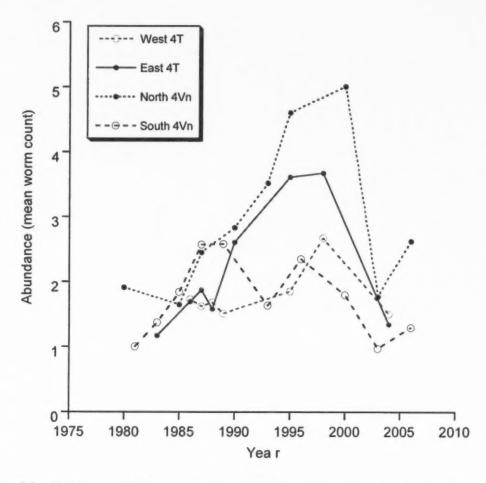


Figure 2.5. Abundance of larval sealworm (Pseudoterranova decipiens) in American plaice (Hippoglossoides platessoides), 31-40 cm in length, sampled from the south-western (west 4T) and south-eastern (east 4T) Gulf of St. Lawrence, the Smokey Channel (north 4Vn) and the slope of the southern Cape Breton Shelf (south 4Vn) between 1980 and 2006.

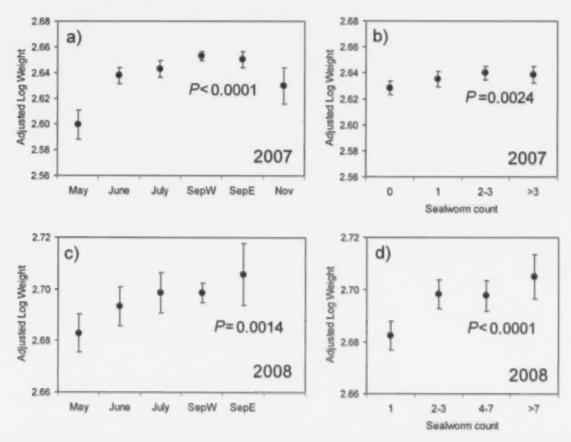


Figure 3.1. Effects of month and sealworm (P. decipiens) abundance on the carcass weight of small (30-44 cm) southern Gulf cod in 2007 and 2008. Circles are the least-squares means (means adjusted to average effects of other independent variable). Results are from a model like that described by equation 3.1, except that sealworm abundance is treated as a factor with 4 levels. P is the significance level for this factor. Vertical lines are 95% confidence intervals. September means are shown separately for eastern (SepE) and western (SepW) regions of the southern Gulf. Samples in other months were restricted to either the east or the west (Swain et al. 2011).

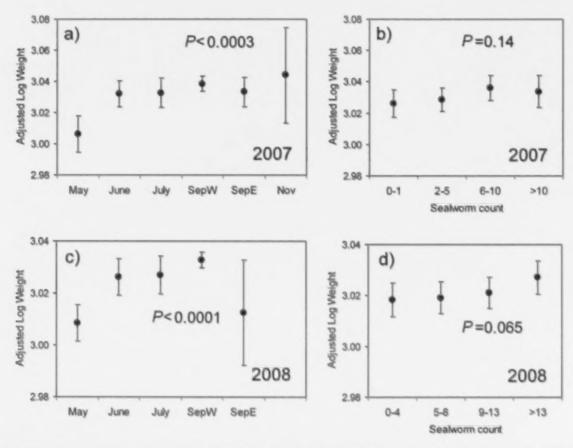


Figure 3.2. Effects of month and sealworm (P. decipiens) abundance on the carcass weight of large (>44 cm) southern Gulf cod in 2007 and 2008. Circles are the least-squares means (means adjusted to average effects of other independent variable). Results are from a model like that described by equation 3.1, except that sealworm abundance is treated as a factor with 4 levels. P is the significance level for this factor. Vertical lines are 95% confidence intervals. September means are shown separately for eastern (SepE) and western (SepW) regions of the southern Gulf. Samples in other months were restricted to either the east or the west (Swain et al. 2011).

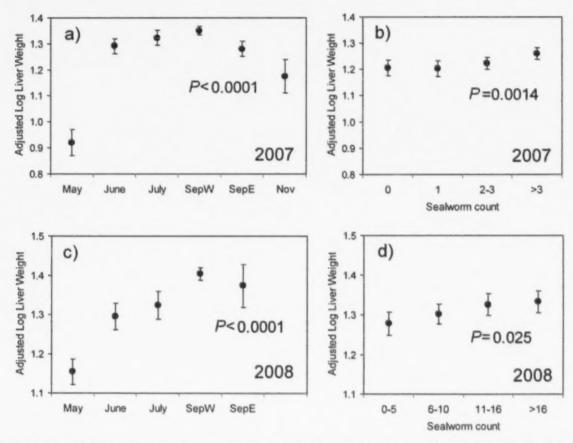


Figure 3.3. Effects of month and total parasite abundance on the liver weight of small (30-44 cm) southern Gulf cod in 2007 and 2008. Circles are the least-squares means. Vertical lines are 95% confidence intervals. Results are from a model like that described by equation 3.1, except that sealworm abundance is treated as a factor with 4 levels. P is the significance level for this factor. Parasites are P. decipiens, A. simplex and, in 2008 only, C. osculatum. September means are shown separately for eastern (SepE) and western (SepW) regions of the southern Gulf. Samples in other months were restricted to either the east or the west (Swain et al. 2011).

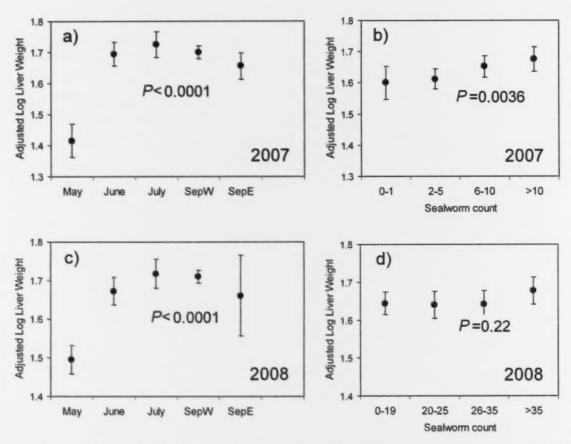


Figure 3.4. Effects of month and total parasite abundance on the liver weight of large (≥45 cm) southern Gulf cod in 2007 and 2008. Circles are the least-squares means. Horizontal lines are 95% confidence intervals. Results are from a model like that described by equation 3.1, except that sealworm abundance is treated as a factor with 4 levels. P is the significance level for this factor. Parasites are P. decipiens, A. simplex and, in 2008 only, C. osculatum. September means are shown separately for eastern (SepE) and western (SepW) regions of the southern Gulf. Samples in other months were restricted to either the east or the west (Swain et al. 2011).

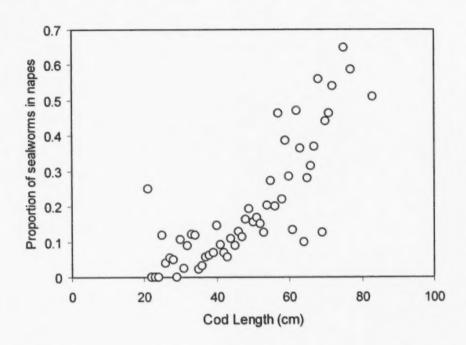


Figure 3.5. Proportion of sealworms occurring in the belly flaps ("napes", the part of the hypaxial muscles forming the abdominal wall) of southern Gulf cod sampled in May 2009.

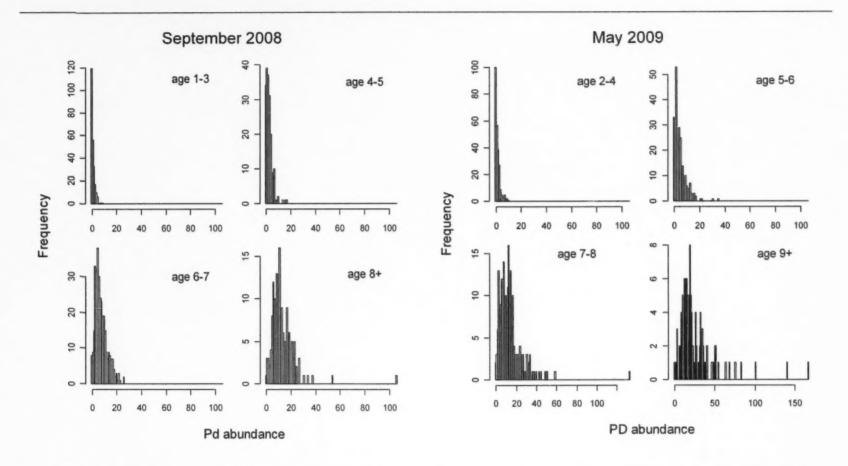


Figure 4.1a. Abundance of Pseudoterranova larvae in age groups of southern Gulf cod collected in September 2008.

Figure 4.1b. Abundance of Pseudoterranova larvae in the corresponding cohorts of southern Gulf cod collected in May 2009. (Age is incremented by 1 yr on January 1.)

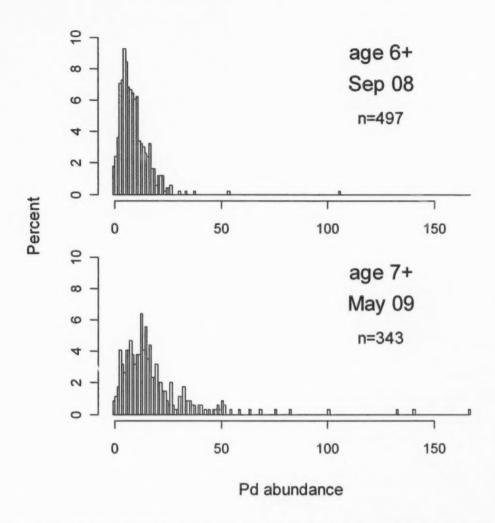


Figure 4.2. Abundance of Pseudoterranova larvae in cod 6 years and older collected in September 2008 and in the same cohorts collected in May 2009.

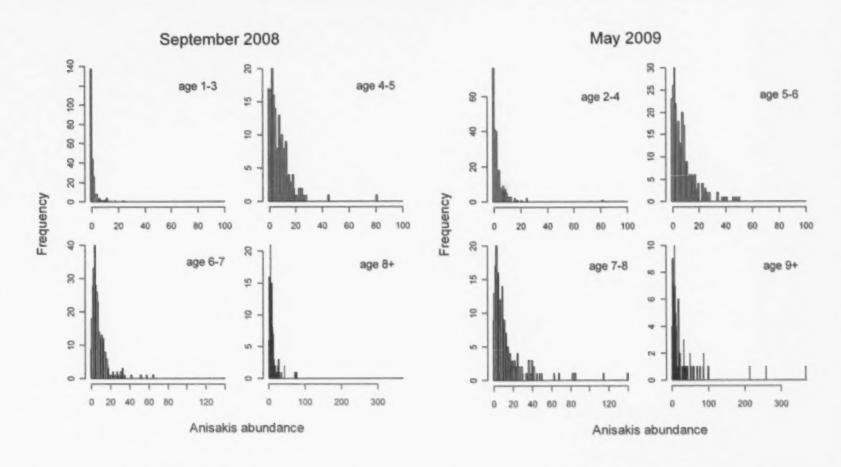


Figure 4.3a. Abundance of Anisakis larvae in age groups of southern Gulf Figure 4.3b. Abundance of Anisakis larvae in the corresponding cohorts of cod collected in September 2008.

Figure 4.3b. Abundance of Anisakis larvae in the corresponding cohorts of southern Gulf cod collected in May 2009. (Age is incremented by 1 yr on January 1.)

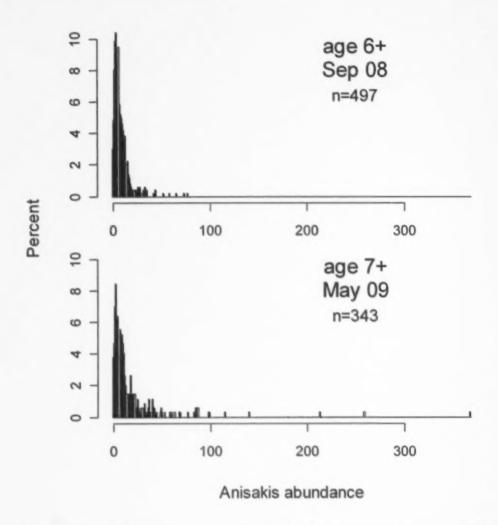


Figure 4.4. Abundance of Anisakis larvae in cod 6 years and older collected in September 2008 and in the same cohorts collected in May 2009.

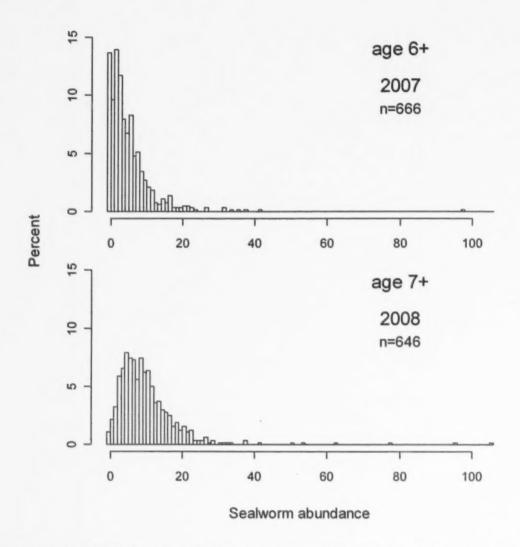


Figure 4.5. Abundance of sealworm (Pseudoterranova decipiens) in cod 6 years and older collected in 2007 and the same cohorts collected in 2008.

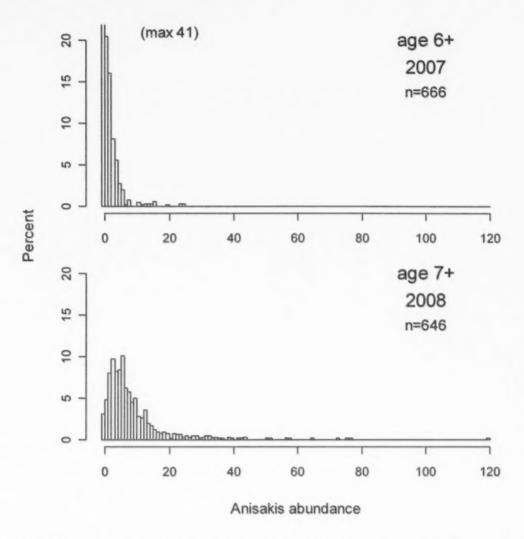


Figure 4.6. Abundance of Anisakis simplex in cod 6 years and older collected in 2007 and the same cohorts collected in 2008.

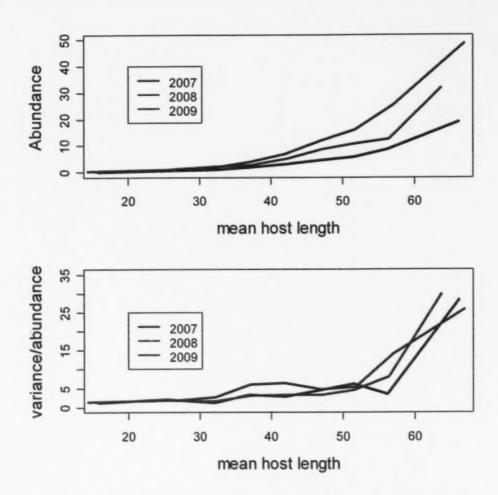


Figure 4.7. Relationships of sealworm abundance (mean count) and variance/abundance ratio to host length by 10 cm length groups of cod sampled from the southern Gulf of St. Lawrence in 2007 to 2009.